Habitat relations in sympatric populations of *Ctenomys australis* and *Ctenomys talarum* (Rodentia, Octodontidae) in a natural grassland

By Viviana M. Comparatore, Mónica Agnusdei, and Cristina Busch

Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

Abstract

Studied the relationship between animal spatial distribution of two sympatric populations of "tuco-tucos" (*Ctenomys australis* and *Ctenomys talarum*) in Necochea (Buenos Aires Province, Argentina), and certain environmental variables. The two species occupy different types of soil and vegetation. *C. australis* inhabits areas with sparse vegetation, sandy and deep soils, while *C. talarum* inhabits areas with dense vegetation, compact and shallow soils. Seasonally, "tuco-tucos" are also associated with fine grain variables, as observed in autumn, where the total number of animals, and the number of *C. australis* individuals, were positively correlated with the abundance of grasses, perennials, plants with reserve organs and creeping habit plants.

Introduction

Biological factors such as interspecific interactions may play an important role in subterranean rodent distribution. There are very few documented cases of sympatry in subterranean rodents (Contreras and Reig 1965; Russell 1968; Reichman and Baker 1972; Williams and Baker 1976; Moulton et al. 1983; Pearson 1984). Vaughan (1967) suggested only one subterranean niche exists for herbivorous mammals. Subterranean mammal distribution, although sometimes parapatric, is seldom sympatric, and since parapatric distribution is determined by competition, it can be predicted that sympatry could be transitory (Moulton et al. 1979).

In the Southern Hemisphere, nearly all *Ctenomys* species ("tuco-tucos") present an allopatric distribution. In Argentina, only two cases of parapatry have been recorded (Pearson 1984; Reig et al. 1990); and only one case of sympatry was registered between *Ctenomys australis* and *Ctenomys talarum* in Buenos Aires Province, from Bahía Blanca to Monte Hermoso, where these two species occupy different soil and vegetation types (Contreras and Reig 1965). We discovered that this distribution extends up to Necochea and that *C. australis* does not live in allopatry in this area. The fact that this situation has been maintained over a long period (Contreras and Reig 1965), the different corporal sizes between *C. australis* and *C. talarum*, and the manifest spatial segregation between both species associated with different soil and vegetation types, all suggest that these populations coexist in sympatry, with non-overlapping niches. Corporal size differences between populations have been documented by Malizia et al. (in press), who determined that *C. australis* weighs three times *C. talarum*.

In the present study, the hypothesis was tested that *C. australis* and *C. talarum* occupy different habitats in the area of sympatry. In addition, it was determined whether different animal categories occupy different habitats according to sex, age and reproductive conditions.

Material and methods

The present study was conducted in a dune natural grassland (VERVOORST 1967; CABRERA and ZARDINI 1978) in Necochea district (Buenos Aires Province, Argentina). The sampling period extended from November 1987 to September 1988. In each season, an area of approximately 2 ha was selected inside the overlap zone of both species. In the area studied in spring, distribution areas of *C. australis* and *C. talarum* were clearly delimited. In contrast, in summer, autumn and winter, the spatial distribution of both species in the chosen areas was more intermingled, showing greater heterogeneity than in spring. Vegetation samples and animals were taken toward the end of each season (November–December 1987, February–March, May–June and August–September 1988). In each area, a 10 by 10 m grid was traced. Vegetation samples were extracted systematically each 10 m. A soil block of 30 cm diameter and 30 cm depth was collected at each sample site. Then, samples were separated by hand in each species aerial and subterranean fractions. The material was dried at 80 °C, and the corresponding dry weights were obtained. A sample by species matrix (aerial plus subterranean biomass/species/sample) was constructed for each season. Twenty-four samples were obtained in spring, 24 in summer, 31 in autumn and 48 in winter.

Density and spatial distribution of both populations of "tuco-tucos" were estimated in a simultaneous study carried out in the same grids, by capture and extraction of all the animals present in the studied area (Table 1). Animal species, localization in the grid, age, sex, weight and reproductive condition were registered (MALIZIA et al. in press). Once during the duration of the study, soil hardness and soil depth overlying the calcareous layer were determined randomly. Twenty five measurements of soil hardness and depth were obtained with a penetrometer and a steel bar, respectively, in both species' zones.

Table 1. **Seasonal densities (individuals/ha) of** ***C. australis*** **and** ***C. talarum***

According to MALIZIA et al. (in press)

	Spring	Summer	Autumn	Winter
C. australis	7.4	4.5	4.0	4.6
C. talarum	10.7	12.7	17.0	4.6

To characterize the vegetation, different bionomic attributes relevant to vegetation spatial heterogeneity and plant-animal interactions were assigned to the plant species. The bionomic attributes considered were: perennity, presence of reserve organs, phenology, pilosity, growth form, presence in modified fields, taxonomic class. Besides ocular observation, the species descriptions of CABRERA and ZARDINI (1978), and LOMBARDO (1982, 1983, 1984) were consulted. With this information, a species by attributes matrix (floristic matrix) was created. This matrix was analysed complementing ordination (Principal Component Analysis, PCA, Harris, 1975) and classification (Cluster Analysis, CA, Orlóci, 1978) techniques so as to describe species variation and define species groups. The CA was performed with Nearest Neighbor distance estimator, simple linkage, and 1-Pearson correlation coefficient for sample distances. Table 2 shows a list of species present in the area grouped according to the analysis just described.

Each seasonal aerial plus subterranean biomass/species/sample matrix was multiplied by the floristic matrix, obtaining an attribute/sample matrix. The four seasonal matrices were appended so as to obtain an annual matrix of data. The importance of each attribute in the samples was also analysed complementing PCA and CA so as to describe the principal trends of vegetation heterogeneity. Sample groups were defined at a level of internal similarity $\geq$ to 80 %.

To determine which vegetation characteristics were associated with animal distribution, simple correlations were established between sample positions along the principal axes of ordination and the total number of captured animals, the number of *C. australis* individuals and the number of *C. talarum* individuals, at each sample site. Also, seasonal sample groups of vegetation, at each seasonal analysis, were related to animal categories which occupied such sites. SYSTAT statistical program was used to analyse data.

Results

Figure 1 corresponds to the annual analysis (samples taken in spring, summer, autumn and winter) and shows the spatial distribution of samples along the first two axes of the PCA on the samples/attributes matrix. All the vegetation variables included in the analysis had positive weights in axis 1, most of them having values over 0.7. Then, axis 1 separates samples with high from samples with low abundance of the plant attributes evaluated, and thus is interpreted as an index of vegetation coverage and density. According to this interpretation, the negative and positive extremes of the axis are denominated "sparse vegetation" and "dense vegetation", respectively. Samples with sparse vegetation have

Table 2. **Vegetation groups, according to ordination and classification techniques, from a dune natural grassland in Necochea district, Buenos Aires Province, Argentina, where *C. australis* and *C. talarum* show an overlap in their distributions**

Group	Attributes	Species
1	Forbs, Annuals, Cool season species, Pivotal roots, Without reserve organs, Present in modifield fields	*Geranium dissectum* *Lepidium bonariense* *Gamochaeta spicata* *Stellaria media* *Melilotus indicus* *Senecio madagascariensis* *Medicago minima* *Medicago lupulina*
2	Forbs, Perennials, Warm season species, Pivotal roots	*Convolvulus hermanniae* *Adesmia incana* *Mesembryanthemum* sp. *Oenothera mollisima* *Achyrocline satureioides* *Margyricarpus pinnatus* *Ambrosia tenuifolia* *Solidago chilensis*
3	Forbs and Grasses, Perennials, With reserve organs, Warm season species, Creeping habit	*Solanum commersonii* *Hydrocotyle bonariensis* *Calystelgia soldanella* *Panicum racemosum* *Paspalum vaginatum*
4	Grasses, Perennials, Glabrous	*Agrostis* sp. *Poa bonariensis* *Sporobolus indicus*
5	Grasses, Fibrous roots, Without reserve organs, Erect habit	*Bothriochloa laguroides* *Stipa neesiana* *Stipa trichotoma* *Bromus* sp. *Lolium multiflorum* *Poa annua* *Hordeum leporinum* *Catapodium rigidum* *Lophochloa phleoides*
6	Annuals, Grasses, Fibrous roots, Without reserve organs, Creeping habit	*Cenchrus pauciflorus*

sandy and deep soils (soil hardness 4.1 ± 0.9 kg/cm^2, and soil depth 80 ± 24 cm), while those with dense vegetation have compact and shallow soils (soil hardness 29.3 ± 8.1 kg/cm^2, and soil depth 57 ± 27 cm). Axis 2 opposes samples whose species attributes are typical of modified fields (annuals, cool season cycle, without reserve organs) to samples whose species attributes are typical of unmodified fields (perennials, creeping habit, with reserve organs). Three groups of samples were defined by CA: 1. Dense vegetation, with plant attributes characteristic of unmodified fields. 2. Dense vegetation, with plant attributes characteristic of modified fields. 3. Sparse vegetation, with plant attributes characteristic of modified and unmodified fields.

Total number of animals, as well as number of individuals of both *C. australis* and *C. talarum* showed a significant correlation ($P < 0.05$) with sample position along axis 1 of the PCA. Total number of animals and number of *C. talarum* individuals were positively correlated with the position of dense vegetation samples, and number of *C. australis*
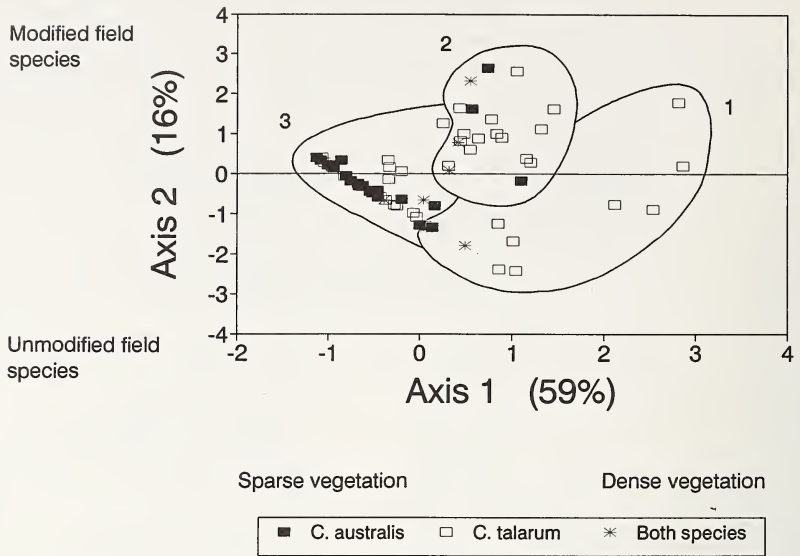
Fig. 1. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Annual analysis. Values in brackets show the percentage of the variance explained by each axis. Symbols indicate presence of *C. australis, C. talarum*, or both species, respectively. Samples without animals were excluded to simplify the diagram. Samples were grouped according to a CA on the referred matrix

individuals was positively correlated with the position of sparse vegetation samples. According to these results, two habitats were defined:
a. Typical *C. talarum* area: dense vegetation, compact and shallow soil;
b. Typical *C. australis* area: sparse vegetation, sandy and deep soil.
C. australis had a body weight three times that of *C. talarum* (males: 425.3 ± 19.8 g vs. 131.6 ± 17.2 g, and females: 297.7 ± 6.8 g vs. 98.7 ± 13.52 g) and a lower population density (5.15 ± 0.76 individuals/ha vs. 11.32 ± 2.56 individuals/ha), MALIZIA et al. (in press).

In the seasonal analysis, as in the annual one, the principal tendency in data variability (axis 1, PCA) shows a contrast between sparse and dense vegetation (Figs. 2, 3). Except in autumn, this contrast explains more than 60 % of the total variance. This shows that two environmental subsystems are clearly distinguishable. In autumn (axis 1 explains 47 % of total variance) the contrast is diluted (Fig. 2). The second tendency in autumn data variability (axis 2, PCA), as well as in the annual analysis, marks a contrast between species attributes typical of unmodified vs. modified fields: grasses, perennials, presence of reserve organs, and creeping habit, vs. forbs, annuals, pivotal roots, respectively. Although less marked, this second contrast also exists during the remainder of the seasons.

The CA of the autumn data shows four groups of vegetation (Fig. 2.): 1. Dense vegetation, with plant attributes characteristic of unmodified fields. 2. Dense vegetation, with plant attributes characteristic of modified fields. 3. Sparse vegetation, with plant attributes characteristic of modified and unmodified fields. 4. Sparse vegetation, mainly characteristic of unmodified fields.

The CA of the spring data shows two main sample groups (Fig. 3): 1. Dense vegetation. 2. Sparse vegetation. Both vegetation types have plant attributes characteristic of modified and unmodified fields. Only four samples are not included in the main groups as a
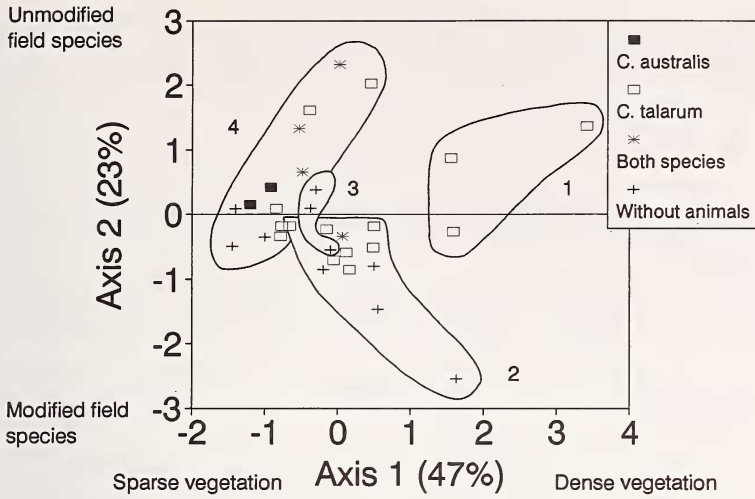
Fig. 2. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Autumn analysis. Values in brackets show the percentage of the variance explained by each axis. Symbols indicate presence of *C. australis, C. talarum*, or both species, respectively. Samples were grouped according to a CA on the referred matrix
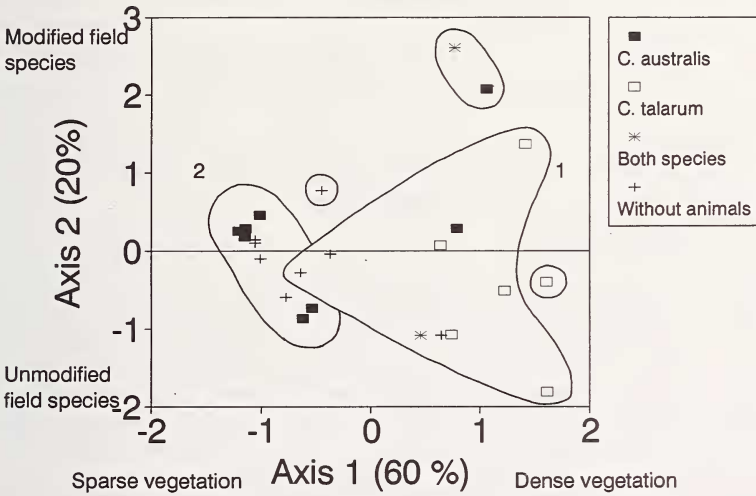

Fig. 3. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Spring analysis. Values in brackets show the percentage of the variance explained by each axis. Symbols indicate presence of *C. australis, C. talarum*, or both species, respectively. Samples were grouped according to a CA on the referred matrix

consequence of some characteristics that are atypical or not relevant in the present context.

In spring, the total number of animals was significantly correlated ($P < 0.05$) with dense vegetation samples, and in autumn with samples that had greater abundance of grasses, perennials, presence of reserve organs and creeping habit. In summer and winter, no significant correlation was found between the total number of animals and vegetation characteristics.

In spring and winter, the distribution of *C. talarum* is more restricted to dense vegetation areas (the number of *C. talarum* individuals showed a significant correlation with position of samples along axis 1, $P < 0.05$), while in autumn and summer its distribution is more dispersed. On the contrary, the distribution of *C. australis* is more restrained in autumn (the number of *C. australis* individuals showed a significant correlation with the position of samples that have greater abundance of grasses, perennials, plants with reserve organs and creeping habit, $P < 0.05$) and in summer (significant correlation with the position of samples that have greater abundance of forbs, glabrous plants, and plants with pivotal roots, $P < 0.05$), while in spring and winter its distribution shows a greater dispersion.

In Figure 4, animal species and animal category distribution was superimposed on to sample distribution along axes 1 and 2 of the PCA on the autumn sample/attribute matrix
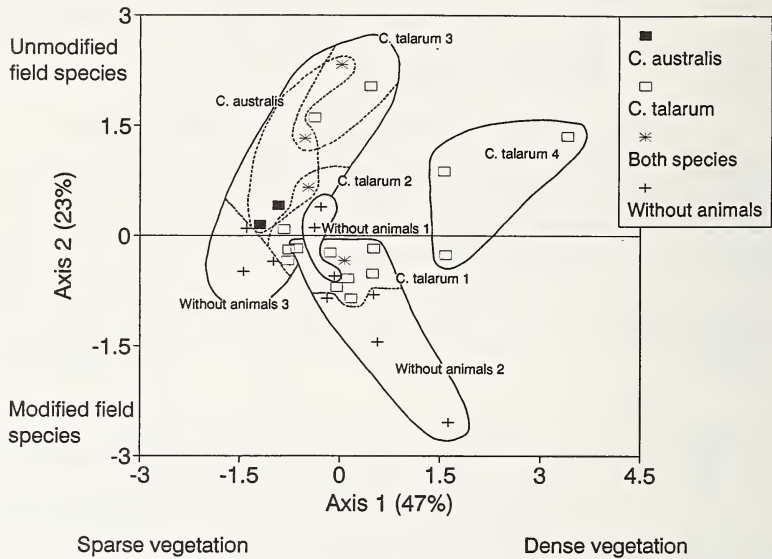

Fig. 4. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Autumn analysis and its relation with animal species and categories. Values in brackets show the percentage of the variance explained by each axis. Samples were grouped according to a CA on the referred matrix. When a vegetation sample group had several animal categories, subdivisions with dotted lines were made. *C. australis* group: 100 % adults; 20 % males; Adult mean weight = 337 g ± 61; *C. talarum* 1: 67 % adults (60 % males); 33 % juveniles (100 % females); Adult mean weight = 119 g ± 21; *C. talarum* 2: 67 % adults (100 % males); 33 % juveniles (100 % females); Adult mean weight = 122 g ± 17; *C. talarum* 3: 80 % adults (100 % males); 20 % juveniles (100 % females); Adult mean weight = 128 g ± 20; *C. talarum* 4: 83 % adults (60 % males); 17 % juveniles (100 % females); Adult mean body weight = 117 g ± 26

(Fig. 2). The spatial distribution of the different animal categories was associated with the existence of vegetation sample groups. Four sample groups with the presence of *C. talarum*, one group with the presence of *C. australis*, and three groups without animals, were defined (Fig. 4). A decrease in the percentage of juveniles and an increase in the percentage of males, was observed through groups 1 to 3 of *C. talarum*. *C. talarum* adult females are only found in groups 1 and 4, whose vegetation presents the greater differences to those of the *C. australis* group. Samples with the presence of *C. australis* and *C. talarum* group 3, which is included in the *C. australis* area, practically do not have annual species, with pivotal roots, present in modified fields. A vegetation gradient is observed through *C.*

talarum groups 1, 2 and 3, where grasses, perennials, plants with reserve organs and creeping habit, become increasingly abundant. This association between animal categories and vegetation was not observed in the remaining seasons.

Discussion

The principal tendency in annual and seasonal data variability shows a contrast between sparse and dense vegetation, as COMPARATORE et al. (1991) observed in an allopatric population of *C. talarum* in a natural grassland in Mar de Cobo district (Buenos Aires Province, Argentina). In the annual analysis, the positive correlation (P < 0.05) between the total number of animals and the position of samples along axis 1 (dense vegetation) could be due to the greater number of *C. talarum* individuals studied (78 animals) compared to *C. australis* (38 animals). This difference is related to the greater density of the *C. talarum* population in the study site than that of *C. australis*, as noted previously. The results indicate that *C. australis* generally concentrates in zones with sparse vegetation, while *C. talarum*, although present in zones with sparse vegetation, concentrates in those with dense vegetation (Fig. 1). Sparse vegetation is associated with sandy and deep soils, having low water retention, while dense vegetation is associated with compact and shallow soils, having higher water retention than the former. These results confirm the hypothesis that subterranean rodent populations can coexist in sympatry by separating niches. This confirms CONTRERAS and REIG's (1965) observations on the same species.

Moreover, the studied sympatric populations greatly differ in their corporal sizes. *C. talarum* adult weight is three times smaller than that of *C. australis* (MALIZIA et al. in press). Similarly, McNAB (1966) observed the greater sized species of pocket gopher has narrower soil tolerances, requiring looser and deeper soils. The smaller species can occupy sandy and deep soils in areas where the larger species is not found, but if the latter one is present, the former would be displaced to marginal and shallower soils. The correlation between the pocket gopher body size and soil texture may be the consequence of a negative correlation between body size and burrow temperature, and therefore be related to thermoregulatory adaptations (McNAB 1966). On the contrary, VLECK (1979) based this correlation on energetic adaptations. Nevertheless, McNAB's (1966) and VLECK's (1979) explanations are not mutually exclusive. BEST (1973) studied the ecology and distribution of three genera of pocket gophers and found the largest species presented the most limited distribution and the broadest range of soil types. The obtained results suggest *C. talarum* has no environmental limitations to occupy typical areas of *C. australis*. When the latter is absent, the spatial occupation of *C. talarum* would be more general. Studying an allopatric population of *C. talarum* in Mar de Cobo district, Buenos Aires Province, Argentina (COMPARATORE et al. 1991), animals occupied soils with hardness varying from 7 to 52 kg/cm². On the contrary, *C. australis* has physiological constraints (BUSCH 1989), due to its greater body size, which impede the occupation by this species of the typical *C. talarum* area.

Vegetation characteristics, where animal species were studied, vary throughout the year. Animal spatial distribution toward the end of spring, is related to the density of vegetation, and toward the end of autumn to the presence of grasses, perennials, presence of reserve organs and creeping habit. This suggests that toward the end of autumn, when vegetation aerial productivity is low, the animals tend to construct feeding tunnels toward areas where the mentioned attributes characterize the vegetation. Most of these plants are green at this time of the year. The results indicate that animals avoid areas with an abundance of annuals, plants with pivotal roots, plants present in modified fields and forbs, which are dry at this time of the year. Conversely, in spring, when vegetation aerial productivity is high, animals prefer areas with dense vegetation with much green material available. Furthermore, in autumn and winter, as a consequence of the lower availability of

aerial biomass, it would be expected that the percentage of vegetation in the subterranean fraction of animal diets would be greater than in spring and summer. This is in accordance with our results on diet preferences of these animals.

In autumn and summer, distribution of *C. talarum* shows greater dispersion. In contrast, distribution of *C. australis* shows a greater dispersion in spring and winter. These results could be related to the density peaks of each species (MALIZIA et al. in press), the density peak of *C. talarum* being in May–June (autumn, where its occurrence is less restricted) and that of *C. australis* in November–December (spring, also coincident with its less restricted distribution).

Results of summer animal capture (MALIZIA et al. in press) were unexpected as far as the type of soil was concerned, since only in this season was *C. talarum* captured in sandy soils. The scarcity of *C. australis* in the summer study site could be explained by the existence of a compact soil barrier that limited its ingress from sandy soil areas where this species was present in high density. In this condition, *C. talarum* occupied both its typical area and that of *C. australis*. This supports what was stated above that the distribution of *C. talarum* is not limited by soil hardness in this area.

In autumn, it could be observed that animal category distribution (juveniles, females, males) varies concomitantly with the vegetation gradient. No similar relationship was detected for other seasons, thus suggesting that during certain periods of the year other factors, such as social behavior or predation, may be stronger determinants of animal distribution.

In conclusion, these sympatric species occupy area of differing types of soil and vegetation. *C. australis* inhabits areas with sparse vegetation, sandy and deep soils, while *C. talarum* inhabits zones with dense vegetation, and compact and shallow soils. Seasonally, *C. australis* and *C. talarum* show a complementation in their spatial distribution. *C. australis* has a greater dispersion in spring and winter, and a greater restriction in summer and autumn. *C. talarum* has a greater dispersion in summer and autumn, and a greater restriction in spring and winter. "Tuco-tucos" are also associated with fine grain variables as observed in autumn, where the total number of animals, and the number of *C. australis* individuals, were positively correlated with the samples that had abundance of grasses, perennials, plants with reserve organs and creeping habit plants. The data suggest that other factors, such as social behavior or predation, may play an important role in animal spatial distribution.

Acknowledgements

Zusammenfassung

Habitatbeziehungen bei sympatrisch lebenden Populationen von Ctenomys australis und Ctenomys talarum (Rodentia, Octodontidae) in natürlichem Grasland

Untersucht wurde die Raumverteilung zweier sympatrisch lebender Populationen von Tukotukos (*C. australis* und *C. talarum*) in Abhängigkeit von Umgebungsveränderlichen in der Nähe von Necochea in der Provinz Buenos Aires, Argentinien. Beide Tierarten leben in Gebieten mit verschiedenen Boden- und Vegetationsarten. *C. australis* bewohnt Gebiete mit wenig Vegetation und sandigem, tiefen Boden, während *C. talarum* Gebiete mit dichter Vegetation und kompaktem, flachgrundigem Boden bewohnt. Die Tukotuko-Populationen wurden auch in Bezug auf andere Variable untersucht: Es wurde im Herbst beobachtet, daß die Anzahl von Tukotukos, insbesondere *C. australis*, positiv mit folgenden Variablen korreliert war: Häufigkeit von Gräsern, ganzjährigen Pflanzen, Pflanzen mit Reserveorganen und von am Boden entlangwachsenden Pflanzen.

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Authors' address: VIVIANA MARTA COMPARATORE, MÓNICA AGNUSDEI and CRISTINA BUSCH, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, C.C. 1245, (7600) Mar del Plata, Argentina